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OBSERVATIONS ON COPULATION AMONG CRAWFISHES WITH SPECIAL REFERENCE TO SEX RECOGNITION

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DURING the past winter the writer kept about three hundred crawfishes in aquaria for a couple of months and had opportunity to observe their copulating reactions from time to time. As the published statements in regard to sex recognition in the genus Cambarus are somewhat meager, the results of some of these observations may be of interest. The species represented in the aquaria were, *Cambarus blandingi acutus* Girard, *C. diogenes* Girard and *C. virilis* Hagen. Most of the observations here recorded were made upon the last-named species, but nothing was observed in the behavior of the others to make it appear that there was any essential difference in the mating reactions of these forms.

Andrews[1] was the first to give a careful account of copulation in the genus Cambarus. He discovered that while the male holds the female on her back beneath him a spermatophore is transferred from his abdominal appendages to the cavity within the annulus ventralis of the female, where it remains sealed up until the eggs are laid. Andrews gives an excellent account of the details of the process but refers only indirectly to sex recognition. He remarks (p. 868):

> When a male is put into a vessel with a female he seems ere long to become aware of the presence of the female and does not act as he does when only males are present. The female generally retreats and may

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[1] Andrews, E. A., "Conjugation in an American Crayfish," AMER. NAT., Vol. 29, 1895, No. 345, pp. 867–873.

even resist the attacks of the male, but generally this is not done with much vigor, and very soon after being seized by the male the female passes into a state of passivity, resembling death.

Hay[2] in a recent paper makes statements which give a somewhat different aspect to the matter. In speaking of an hermaphrodite crawfish he says (p. 228):

> It might be added that during the time the specimen was kept alive it was seen in conjugation with a female of the same species and a little later was itself seized and held for a short time in the usual manner by a male. The latter, however, is a matter of little importance, as I have several times observed the same thing in the case of two males neither of which was hermaphrodite.

An adult male of the genus Cambarus is easily distinguished from a female of the same species by his larger chelæ and narrower abdomen, and the sex of any individual can of course be accurately determined by examining the first two pairs of abdominal appendages. Whether such differences are as readily discriminated by the sensory receptors of a crawfish as they are by the human eye is perhaps open to question. According to the quotation from Andrews it would appear that a male is able to recognize a female as such, but the statements of Hay might be interpreted in such a way as to lead to the opposite conclusion.

A series of five experiments was carried out to test the ability of male crawfish to discriminate members of the opposite sex. In the different experiments from two to seven males were separated from females which they had been holding and put together in a flat circular dish (which measured thirty centimeters in diameter and contained clean water to a depth of about five centimeters). After such treatment the crawfishes were active for a time and moved restlessly about the dish. During this period of activity one male often tried persistently to copulate with another male, but such attempts were always resisted, and, although individuals were turned over in some cases, they always eventually succeeded in freeing themselves. After these males had been allowed to " fight " thus among themselves for from half an hour to two hours (the time varied in different experiments) they became comparatively quiet and finally came to rest in a group at one side of the dish in such a way that their bodies were in contact with each other. After they had remained in this condition of rest for at least half an hour a female which had just been released from copulation with a different male was gently introduced into the dish with them.

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[2] Hay, W. P., "Instances of Hermaphroditism in Crayfishes," Smithsonian Misc. Coll., Vol. 48, 1905, Pt. 2, No. 1593, pp. 222–228.

In all five of the experiments the female moved about the dish and came in contact with one or more of the males, and sometimes she even walked over them, but nevertheless there were only two attempts at copulation within half an hour after a female had been placed in the dish. In one of these cases a male attempted to grasp another male after the female had been introduced, but he soon desisted from the attempt and all the individuals in the dish then became quiet again. In the other instance one of the (two) males attempted to turn over the female as soon as she came in contact with him (not as soon as she was introduced into the dish). These experiments showed that males which had recently been in active copulation were not necessarily induced to copulate again by the immediate presence of an active female.

Five other experiments were performed which were similar to those just described except for the fact that the female was introduced into the dish with the males before they had come to rest. In this second series copulation took place within half an hour in every case. The results make it appear that the readiness with which copulation is undertaken by a pair of crawfishes depends upon the physiological state of the male, for, as Andrews has stated, the male usually takes the active part in the mating reactions, while the female remains passive.

Another series of observations showed that the readiness with which copulation takes place depends largely upon the "chance" coming in contact of two individuals which are in proper physiological state. On five different occasions when the aquarium, which contained two hundred crawfishes, was visited and no pairs were found to be copulating or attempting to do so, all the individuals were dragged into the center of the aquarium and heaped together in a pile. They were then allowed to remain undisturbed for half an hour. During this time there was an active scramble and many individuals necessarily came in contact with each other. In all the experiments from three to five pairs were found to be in copulation at the end of the half hour. These observations showed that individuals had been present in the aquarium which were in the proper physiological state for copulation, for as soon as they came in contact with each other the usual mating reaction took place.

There are many factors which might possibly exert an influence on the copulatory reflexes of a crawfish and it is easily conceivable that such stimuli as temperature, light and chemical substances might be of importance in this connection. In regard to temperature Bell[3] has observed (p. 625) that, after a number of individuals had been warmed,

> The males showed marked sexual activity, rushing up to the females, pushing them about, seizing them and trying to turn them over in spite of their vigorous resistance. One of the males did succeed in turning a female on her back twice, although she struggled violently to escape—a thing which a female never does in the ordinary sexual act.

He concluded that, "the rise of temperature seemed to stimulate the males to sexual activity but not the females." During the present experiments it was observed that there were fewer cases of copulation when the temperature of the water in the general aquarium was below 11° C. than when the temperature was above that point. Apparently temperature is of some importance as exerting an inhibitory or excitatory action on the copulatory impulse.

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[3] Bell, J. C., "Reactions of the Crayfish," Harvard Psychol. Ser., Vol. 2, 1906, pp. 615–644.

Chidester[4] has recently shown that the general activity of crawfishes is greater at night and it would therefore seem probable that copulation would be more likely to take place in the dark than in the light. In order to ascertain if this supposition was correct, two oblong dishes were placed side by side in front of a window and were filled to a depth of five centimeters with water which was of the same temperature in the two dishes (11° to 14° C. in different experiments). One of the dishes was allowed to remain exposed to strong light, but not to the direct rays of the sun, and the other was completely enclosed in a tight wooden box which was painted black on the inside and covered by a movable lid. In each experiment two pairs of crawfishes which had been copulating or attempting to do so were isolated and a separate male and female placed together in each dish, after which their behavior was noted at short intervals of time. In order to eliminate the effects due to the individuality of any particular crawfish, the individuals of each quartette were changed about as much as possible in successive trials. After the first copulation, the male was changed from the dark dish to the one in the light, and the male which had been in the light took his place; after the next trial the pairs were interchanged, and finally the two females were changed about. By this method of procedure there was an opportunity to compare the rapidity of copulation in the light and in the dark. The results of the experiments are given in Table I.

TABLE I.

Showing the results of seven experiments to ascertain whether certain crawfishes would copulate more quickly in dark or in light. (L indicates that the pair in the light copulated first; D, the pair in dark copulated first; E, both pairs copulated at the same time.)

Experiment.		1	2	3	4	5	6	7
Trial 1		L	D	L	L	L	D	D
Trial 2	♂ ♂ interchanged	D	E	D	L	L	L	D
Trial 3	Pairs interchanged	L	L	D	D	D	D	D
Trial 4	♀ ♀ interchanged	L	E	L	D	L	D	D

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[4] Chidester, F. E., "Notes on the Daily Life and Food of Cambarus bartonius bartoni," AMER. NAT., Vol. 42, 1908, No. 503, pp. 710–716.

In twelve of the trials copulation took place first in the light; in fourteen cases the pair in the dark copulated first, and in the other two instances the two pairs occupied the same period of time in becoming united. Twenty-eight different individuals were given twenty-eight opportunities to copulate and approximately an equal number of " first " copulations took place in the light and the dark. From these experiments it appears that conditions of light stimulation are apparently of little consequence, at least where individuals which are in a state of excitement are concerned.

Attempts were made to arouse males to a state of activity by adding extracts to the surrounding medium. The males were separated from their mates and allowed to become quiet in a dish of clean water. Various portions of females which had been recently copulating were then added, and although pieces of ovary, pieces of abdomen and extracts from these organs and from the whole body were used in this way, nothing but negative results were obtained. The males remained quiet and exhibited no signs of excitement within half an hour after the portions of the female's body had been added. From these results it does not seem probable that copulation is brought about by the action of any secretion given off by the female which might serve to excite the male.

The results of all the experiments described indicate that sexual union is more or less a matter of chance. If a male and a female which are in the proper physiological condition come together they will copulate with equal readiness in the light or dark. Neither sex can be said to be wholly responsible for the act of sexual union and although the male usually assumes the active part, it is not an invariable rule. An instance was observed in which one female fought almost continuously with another for over two hours. When this pugnacious individual was placed in a dish with several males she walked about actively and grasped them with her chelæ, but as soon as one of them grasped her and attempted to turn her over, she became quiet and was soon in copulation. If we examine Table I it will be seen that in experiments 1 and 6 the same male copulated first in four of the trials, but in experiments 2, 4 and 5 the male which copulated first in trial 1 was equalled or excelled by the rival male in the three succeeding tests. No female copulated first in all four trials.

In all the observations cited no evidence was seen which would go to show any power of sex descrimination in the crawfish. During the mating season the instinct of the male is to grasp and turn over every crawfish which comes in his way. The method is one of trial and the result of such random movements depends largely upon the reactions of the individual with which copulation is attempted. If this individual is a female of the same species the attempt may meet with success but if it is a male or a female of another species the effort at sexual union is usually of short duration. The lack of discriminative ability on the part of the males is shown by the fact that they often attempt to copulate with individuals of their own sex. This fact in itself is not of course very conclusive as similar behavior is often observed in many higher animals, such as dogs and cattle, in which the males are doubtless able to recognize the females as such. Furthermore, on two occasions males were observed to be in copulation with females which had been dead for twelve hours and in another instance a male of one species (*Cambarus virilis*) was found in copulation with a dead female of another species (*C. blandingi acutus*). This last observation is of especial interest for, as Andrews[5] says (p. 474) it is not known "whether the male stylets and the female annulus are closely adjusted to each other in each species or not. Experiments should at least decide whether the males of one species can fill the annuli of other species or not." The observation just cited shows that two different species can at least unite sexually as I was careful to observe that the stylets of the male were actually inserted into the annulus of the female. Whether a spermatophore can be transferred under such circumstances is of course still a question.

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[5] Andrews, E. A., "The Annulus Ventralis," Proc. Boston Soc. Natur. Hist., Vol. 32, 1906, No. 12, pp. 427–479, pl. 43–48.

The observations described in this paper would lead to the conclusion that the crawfishes have little or no power of sex discrimination. The male " tries " every crawfish which he meets and the instinct of the female is to remain passive under such treatment while another male will attempt to escape. The sexes come together as the result of random movements or in the course of the daily travelling about in search of food. Holmes[6] reached similar conclusions as a result of his observations on amphipods. Male amphipods, however, would not attempt to copulate with a dead female and in this respect their powers of discrimination apparently excel those of the crawfish.

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[6] Holmes, S. J., " Sex Recognition among Amphipods," *Biol. Bull.,* Vol. 5, 1903, No. 5, pp. 288–292.